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HABITAT-RELATED DIFFERENCES IN NECROPH- ILOUS SPECIES COMPOSITION: IMPLICATIONS FOR RESOURCE COMPETITION

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HABITAT-RELATED DIFFERENCES IN NECROPHILOUS SPECIES COMPOSITION: IMPLICATIONS FOR RESOURCE COMPETITION—Competition for resources is one of the most important selective factors influencing the expression of life history traits in both plants and animals (Darwin 1859). In grasslands, competition for resources such as nutrients, water, and space often is constrained by stochastic processes (Axelrod 1985). Disturbance factors such as fire, grazing by large herbivores, and fluctuating climatic conditions tend to alter the structure and magnitude of competition for limited resources among grassland communities more frequently than in other ecosystems (Snaydon 1987, van der Maarel 1993). Vertebrate carrion is one important resource used by both plants and animals in grasslands, providing a rich but ephemeral point source of nutrients (Towne 2000, Barton et al. 2013). A complex ecological network of vertebrate and invertebrate necrophilous animal species compete intensely for these carrion resources, often aided by specialized sensory and motility adaptations that aid resource discovery and sequestration (Putman 1978, Scott et al. 1979, DeVault et al. 2003).

One important family in the guild of invertebrate scavengers that compete for vertebrate carrion in both grasslands and forested ecosystems are carrion beetles (Coleoptera: Silphidae). Representing approximately fifty North American species divided into two subfamilies, Silphinae and Nicrophorinae, species in the carrion beetle family are important for their role in nutrient cycling (Scott 1998). One particular group of carrion beetles, the burying beetles in the genus *Nicrophorus*, are well-represented in temperate grasslands and forests in North America with fifteen described species, and their species distributions, habitat preferences, and foraging behaviors are thought to represent an example of classic niche segregation (Wilson et al. 1984, Kocárek 2001, Bishop et al. 2002). Nicrophorine burying beetle adults search for carrion in flight, and compete intensely with congeners, non-Nicrophorine carrion beetles, flies, and ants to secure a carcass resource before discovery by vertebrate scavengers (Pukowski 1933). Upon locating and securing a small vertebrate carcass, typically within a few hours of deposition, a burying beetle male-female pair will bury the carrion for use in reproduction, providing bi-parental care to the developing offspring as they feed on the carcass (Scott 1998). While studies have examined interspecies competition in *Nicrophorus* burying beetles (Wilson and Fudge 1984, Trumbo 1990, 1994), it is not clear how this invertebrate competitive environment differs between grassland and forest habitats. Aggregation and coexistence theory (Hanski 1987, Ives 1991, Woodcock et al. 2002) provides a useful hypothetical framework that explains differences in inter- and intraspecific competition for carcasses in relation to habitat and spatial dynamics. While it is generally thought that vertebrate competition for carrion is higher in forests than grasslands (A. Smith, Northeastern State University, personal communication), altering the competitive dynamics faced by forest-dwelling versus grassland burying beetle species, this conceptual model lacks definitive empirical data.

Thus, our objective was to compare potential competition for carrion between grassland and forested sites, with an emphasis on quantifying the strength of competition among Nicrophorine burying beetles, non-Nicrophorine carrion beetles, and vertebrate scavengers by documenting abundances at traps baited with carrion. Consistent with aggregation and coexistence theory and preliminary data from field studies in the region, we hypothesized that competition would be greater in grasslands among the focal invertebrate groups, and greater in forests among vertebrate necrophilous species, with the prediction that trap abundance data would reflect these hypothetical patterns.

We conducted the study between 26 June and 14 August 2014 at two study sites in Oklahoma: The Nature Conservancy's Tallgrass Prairie Preserve (TPP) in Osage County (890194 E, 4124689 N, 40 sampling sites); and the Muddy Boggy Conservation Bank (MBCB) in Pontotoc County (915966 E, 3958949.48 N, 16 sampling sites; Fig. 1). The TPP site is a 16,000 ha restored prairie consisting of 80% tall and mixed grass prairie species dominated by C_4 grasses, with 20% of the site covered in small cross timber gallery forests (Madsen 1990). The site is managed using prescribed burning, bison grazing, and limited cattle grazing in a patch-burn context (Hamilton 1996). The MBCB site is 1,400 ha bordering the southern tallgrass prairie ecosystem in Oklahoma and consists of 80% cross timber forests, dominated primarily by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*). The site also includes small, anthropogenic grassland inholdings that were excluded from sampling in this study. The MBCB site is designated as a U.S. Fish and Wildlife Service (USFWS) approved mitigation bank for the federally-endangered American burying beetle (*N. americanus*; ABB) and is managed through prescribed burning and traditional forest management techniques such as thinning and targeted biomass reduction. The study sites were selected as they exhibit similar annual (92.5 cm vs. 91.3 cm) and seasonal rainfall (30.8 cm vs. 33.8 cm) and temperature statistics (14.4° C vs. 16.1° C; Oklahoma Mesonet 2013), have similar general soil types (sandy-loams) and elevations (250 m vs. 265 m), and both have documented occurrences of ABBs along with seasonally abundant populations of other vertebrate and invertebrate necrophilous species.

To assess the strength of competition among Nicrophorine and non-Nicrophorine carrion beetles at the two field sites, we assessed focal species abundance as a proxy for competition by installing above-ground baited pitfall traps approved by the United States Fish and Wildlife Service for use in surveys for ABBs. Traps consisted of 18.9-liter buckets with a removable 61 × 61 cm trap cover that contained a bait enclosure (per Leasure et al. 2012). We sampled each site for five days with a single trap baited with an aged pig heart cut into

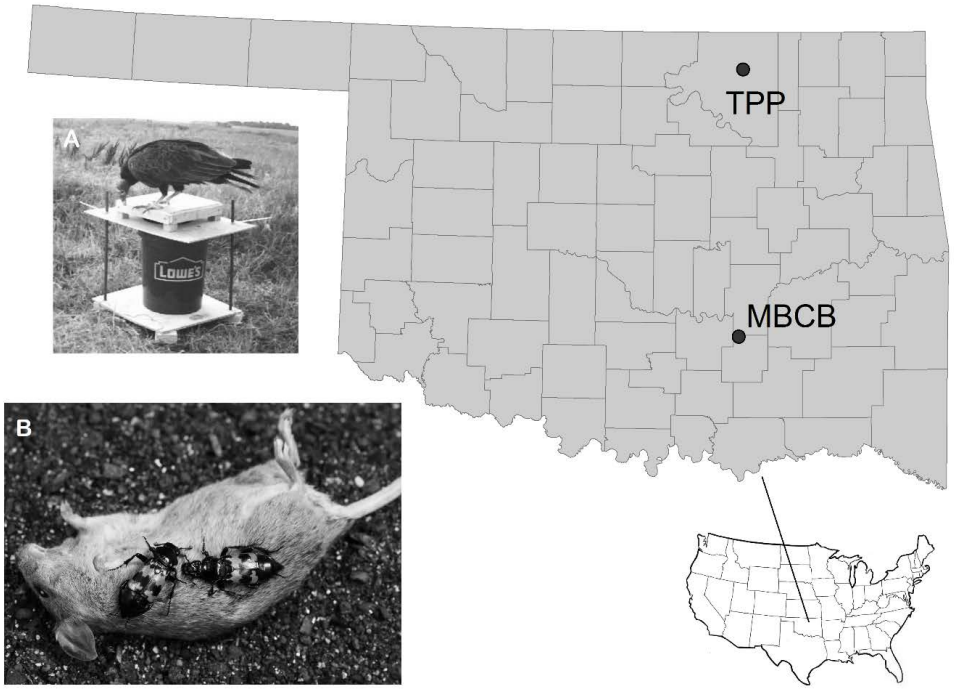

Figure 1. Field site localities in eastern Oklahoma, USA where our carrion competition study was conducted between 26 June and 14 August 2014. To characterize competition for carrion resources in a grassland environment, data was collected at The Nature Conservancy's Tallgrass Prairie Preserve (TPP) in Osage County, Oklahoma. Comparable forest data was collected at the Muddy Boggy Conservation Bank (MBCB) in Pontotoc County, Oklahoma. Inset image A shows a turkey vulture attracted to the bait of an above-ground pitfall trap used to collect necrophilous invertebrates in the study. Inset image B shows a pair of *Nicrophorus marginatus* burying beetles preparing a mouse carcass for burial. Both images taken by DRH.

2.5-cm cubes. Bait was refreshed after three days or as needed due to decomposition. We checked traps each morning before 1000 hr and recorded Nicrophorine and non-Nicrophorine carrion beetle abundance. We marked and released all beetles at the site, and we did not consider recaptures in abundance calculations. We assessed the strength of competition among vertebrate scavengers using motion-activated camera traps (Browning Dark Ops, Model# BTC-6, Morgan, Utah, USA) at each of the trap sites during the five-day trapping period. Vertebrate scavenger presence at a trap triggered the collection of a ten-second digital video recording. We examined all recordings using Kinovea version 0.8.15 videographic analyses software (available free at www.kinovea.org) to identify the presence (Y/N) of vertebrate species of record for each video collection event. We excluded vertebrate species not known to scavenge for carrion but captured in video recordings from analyses. We used Mann-Whitney U Tests to compare abundances expressed as trap-rates (beetles trap-night^{-1}) of Nicrophorine and non-Nicrophorine carrion beetles between grasslands and forested sites, and we used a Fisher's Exact Test to compare vertebrate scavenger presence between habitat types. We compared vertebrate scavenger assemblages between grasslands and forests using the results of a chi-square likelihood ratio test on a contingency table of proportions. All tests were two-tailed, and data were analyzed in SPSS version 21 (IBM Corporation 2012) and JMP version 10 (SAS Institute 2007).

We captured a total of 889 Nicrophorine burying beetles representing five species (*N. americanus, N. marginatus, N. orbicollis*, *N. pustulatus,* and *N. tomentosus*), and 6,229 non-Nicrophorine carrion beetles represented by primarily four genera (*Necrodes, Necrophila*, *Oiceoptoma*, and *Thanatophilus*) at the two study sites. We found greater Nicrophorine burying beetle abundance in the forested versus grassland sites (Fig. 2; U = –2.72, $P = 0.006$, $n = 275$), but found the opposite pattern when examining non-Nicrophorine carrion beetle captures (U = 4.69, $P < 0.001$, $n = 275$). After combining Nicrophorine and non-Nicrophorine carrion beetles to evaluate total invertebrate scavenger abundance, we found higher potential invertebrate competition for carrion in grasslands versus forests (U = 3.41, $P = 0.001$, $n = 275$). The proportion of traps visited by vertebrate scavengers in forests (24%) was similar to that in grasslands (19%; $P = 0.236$). Vertebrate scavenger assemblages differed between the two sites ($\chi_1^2 = 21.61$, $P = 0.001$, $n = 64$), with grasslands dominated by black (*Coragyps atratus*) and red-headed turkey

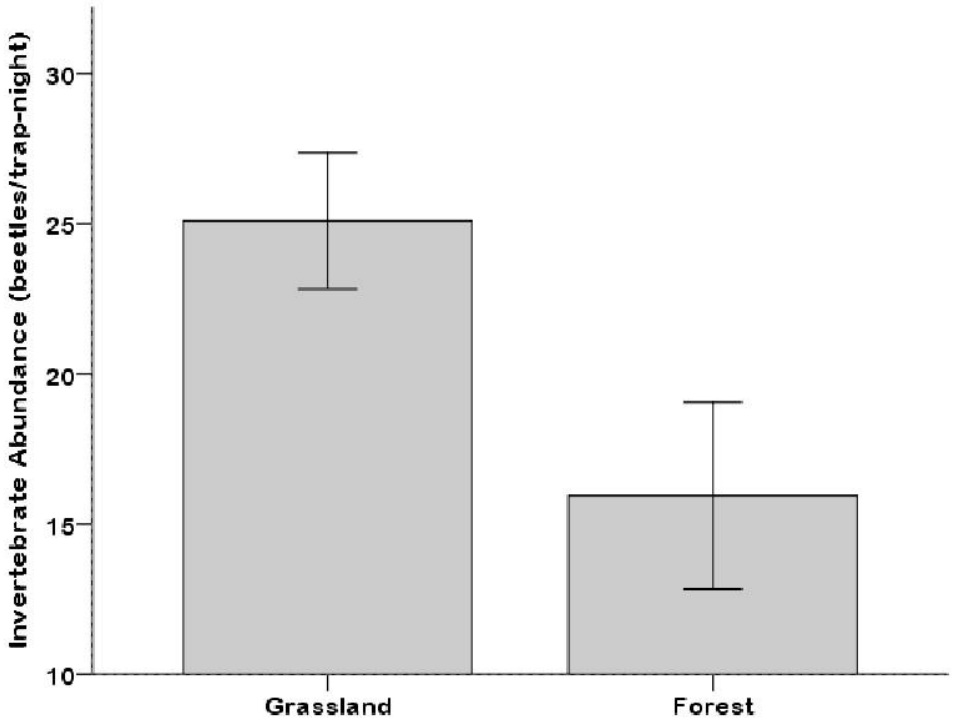

Figure 2. Necrophilous beetle abundances collected between 26 June and 14 August 2014 at the two field study sites in Oklahoma. We found higher invertebrate competition for carrion in grasslands versus forests (Mann-Whitney U = 3.41, $P = 0.001$, $n = 275$). Bars represent ± 1 standard error of the mean beetle abundance (beetles captured trap night^{-1}).

vultures (*Cathartes aura*; 76.7%), followed in proportion by coyote (*Canis latrans*) and nine-banded armadillo (*Dasypus novemcinctus*; both 6.9%), shrews (*Blarina hylophaga*, *Cryptotis parva*; 4.7%), Virginia opossum (*Didelphis virginiana*) and feral dogs (*C. domesticus*; 2.3%). The forested study site exhibited more species evenness with respect to vertebrate scavenger competition, with black and red-headed turkey vultures remaining the most common trap visitor (52.4%), followed in proportion by Virginia opossum (23.8%), common raccoon (*Procyon lotor*; 19.1%), and nine-banded armadillo (4.8%).

Our findings supported our prediction that invertebrate competition for carrion resources in grasslands is potentially greater overall than that observed in forested habitats. Abundance and trap rates of necrophilous beetles in grasslands were nearly double that of forests, with the most common carrion beetle species observed being *Necrodes surinamensis* (the red-lined carrion beetle), which was found in high abundances in grasslands but was of low occurrence in forests. We did not, however, expect to find that overall abundance of Nicrophorine burying beetles was significantly higher in forest than in grasslands. Of the five species of *Nicrophorus* captured in the study, only *N. marginatus* was found in higher abundances in grasslands. Niche segregation dynamics may explain these findings, as the four nocturnal *Nicrophorus* species found in higher abundances at the forested study site may avoid direct competition for carrion with the nocturnal and grassland abundant *N. surinamensis* through exploiting a forest niche. *N. marginatus*, one of the few diurnal Nicrophorine burying beetle species, may avoid direct competition with *N. surinamensis* through temporal niche segregation mechanisms. Aside from *N. pustulatus*, which can reproduce on reptilian eggs (Blouin-Demers et al. 2000), the other four *Nicrophorus* species captured in the study are thought to overlap in carcass size utilization and thus we assume face direct interspecies competition for carrion resources.

We did not, as expected, find greater competition for carrion from vertebrate scavengers in forests, with equal occurrences of trap visits at grassland sites. This conflicts with the commonly held reasoning that the three dimensional structure of forests naturally provides greater refugia for mesopredators like raccoons and opossums, which should therefore lead to higher competition for carrion resources in forests (DeVault et al. 2004). We found that while mammalian predation *per se* was greater at the forested site, the abundance of avian scavengers that foraged across the grassland sites may balance overall vertebrate competition for carrion resources between the two habitats. Differences in vertebrate scavenger assemblages between grasslands and forest habitats likely lends an important temporal component to

resource competition intensity gradients, with greater competition for carrion during the day and lower levels at night in grasslands, with the opposite pattern emerging in forests.

While our study suggests that competition for carrion resources in grasslands is higher overall than that in forests, due primarily to the abundance of necrophilous beetles belonging to the subfamily Silphinae, it is also likely affected by other biotic and abiotic factors not under study in this investigation. We did not account for potential competition from dipteran or hymenopteran insect species, which can be important necrophilous competitors in natural settings but whose effects were controlled for by the bait enclosure in our trap design. Local climatic conditions exert indirect but substantial effects on invertebrate foraging behavior that can also constrain or facilitate competition. The stochastic nature of grasslands, structured by the random and interacting effects of disturbance factors that can directly and indirectly contribute to carrion availability, can lead to unpredictable shifts in carrion-dependent species complexes and their resulting competitive landscape over time (Kneidel 1984, Hanski 1987, Farwig et al. 2014).

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